THE FORM AND NATURE OF THE MUSCULAR CONNECTIONS BETWEEN THE PRIMARY DIVISIONS OF THE VERTEBRATE HEART.

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Introductory.—In a paper contributed to the *Lancet* some months ago (5), the writers confirmed and extended the discovery of Tawara (7), viz. that there is within the mammalian heart a system of peculiar musculature (the a.-v. system) which, beginning as a small root (the *Knoten*) in or near the base of the interauricular septum on the right side, eventually spreads out in an arborescent form beneath the endocardium of both ventricles, its final twigs becoming everywhere continuous with the ordinary musculature of the ventricles. It seemed to us essential to examine other regions of the heart for such peculiar musculature. Moreover Wenckebach (8) has demonstrated by exact clinical methods that a delay may occur in the conduction of the cardiac impulse from sinus to auricle. This fact stimulated us to investigate fully the nature of the muscular connection between the sinus and the auricle, which has already been partly described by Wenckebach in the human heart.

In this paper therefore the writers propose to deal with the results of an extended inquiry, made with three objects in view:—

I. To ascertain the extent, nature, and position of the muscular connection or connections between the primary divisions of the heart in all classes of the vertebrate kingdom.

II. To seek in the sinus, auricle, and bulbus cordis for a differentiation in form and structure of a system of muscle fibres corresponding to that now known to exist in the ventricle: in short, to ascertain whether the musculature in which the heart-impulse is held to arise, and by which it is conducted, differs in form and structure from that which is mainly contractile in nature.

III. To trace the evolution of the a.-v. muscular system, as found in the human heart, from the simpler and more definite form seen in the heart of fishes.

Material.—It is important that those who may consult this paper should know the exact material used by us in this inquiry, and its method of preparation. In the appended list of material we do not include the numerous hearts which have been dissected by knife and forceps, but only those which have been examined by a series of microscopic sections.

List of Material.

Fishes.—Eel, dog-fish, salmon.

Amphibia.—Frogs (3).

Reptilia.—Lizard (species unknown), tortoise, turtle.

Birds.—Sparrows (2), goldfinch.

Mammals (other than human).—Mole, porpoise, dolphin, kangaroo, wallaby, whale (*B. musculus*), mouse, shrew-mouse, rat (2), kitten (2), ram, pig, cart-horse, pony, fœtal gibbon.

Human.—Embryos (2), normal hearts, malformed hearts, and fifteen hearts having definite pathological lesions.

Method of Preparation.—For macroscopic specimens for dissection a modification of Kaiserling's method was used. The great advantage of this method is that the natural colour of the muscle fibres returns after fixation, thereby rendering easier the dissection of the different systems of muscle fibres. The procedure is as follows:—

(1) The heart must be well washed in running water for 12 hours prior to fixation, and the cavities stuffed with tow or cotton-wool.

(2) The specimen is then fixed in the following solution:

Formalin, 200 c.c.
Water, 1000 c.c.
Potassium nitrate, 15 grams.
Potassium acetate, 30 grams.

In this solution it remains at least 24 hours, and longer if it be large, hard, or tough.

(3) Specimen placed in 80 per cent. spirit until its colour returns.

(4) Kept in equal parts of glycerine and water.

In the preparation of microscopic specimens stages (3) and (4) are omitted. After (2) the specimen, or the desired parts of it, is well washed in running water. It is then transferred to spirit (24 hours), next alcohol in stages from 70–100 per cent. for 24–48 hours, then in xylol until clear, and finally embedded in paraffin. We have found that the process of embedding is much facilitated by exhausting the incubator. By this means clear, firm blocks with no trace of air-bubbles are obtained. The blocks were cut in the main at 10 μ, except when it was desired to study the minutest structure of the specimen, when they were cut from 4 μ to 7 μ in thickness, according as the nature of the tissue permitted. The sections were stained by Ehrlich's acid hæmatoxylin and Van Gieson's stain, dehydrated, and mounted in Canada balsam. It is important to overstain with hæmatoxylin, otherwise the nuclei will not be well seen, owing to the decolorising action of the second stain.

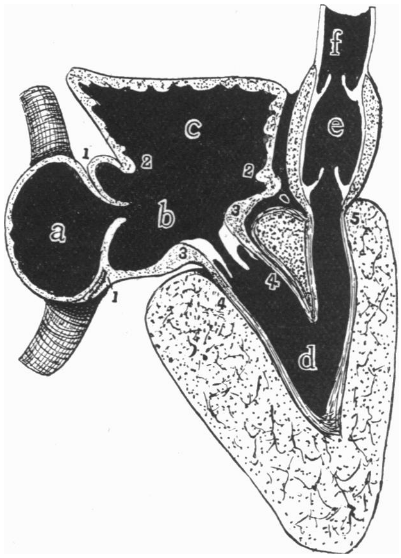

FIG. 1 —Diagram of a generalised type of vertebrate heart—combining features found in the eel, dog-fish, and frog—showing the primary cardiac chambers and their lines of union.

a, sinus venosus and veins ; *b*, auricular canal ; *c*, auricle ; *d*, ventricle ; *e*, bulbus cordis ; *f*, aorta ; 1-1, sino-canalar junction and venous valves ; 2-2, canalo-auricular junction ; 3-3, annular part of auricle, containing special muscle fibres; 4-4, invaginated part of auricle ; 5, bulbo-ventricular junction. By the longitudinal fibres lining the ventricle there is a connection between the annular fibres of the auricle and the bulbus musculature.

Literature.—With regard to literature, we have been unable to find any previous paper approaching the nature of our research. The writings of Gaskell (2), MacWilliam (6), and Engelmann (1) have proved of great service. We accept the teaching (1) that the heart's impulse is conducted by the cardiac muscle tissue, (2) that normally the impulse arises in the musculature of the sinus, setting the heart's rhythm, and then passes to the auricle and ventricle, finally reaching the bulbus cordis.

The Primary Divisions of the Vertebrate Heart.—Before proceeding to describe the muscular connections between the primary divisions of the heart, it is necessary for us to define exactly what we regard as such.

They are well seen in the generalised diagram (fig. 1). There are five primary divisions of the heart:—

(1) The sinus venosus (*a*).
(2) The auricular canal (*b*).
(3) The auricle (*c*).
(4) The ventricle (*d*).
(5) The bulbus cordis (*e*).

There are four junctional lines:—

(1) *The Sino-canalar*, marked by the venous valves, the free margin of the valves forming the boundary-line between the cavity of the sinus and the cavity of the auricular canal (1–1 in fig. 1).

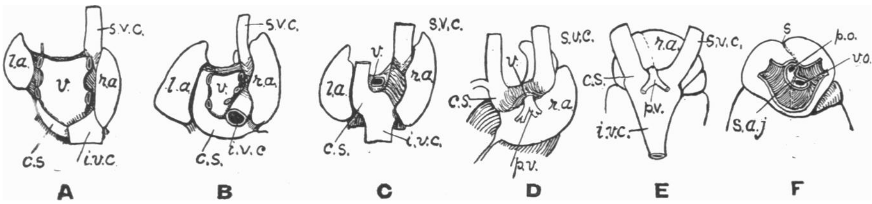

FIG. 2.—Series of diagrams to illustrate the parts in the human heart corresponding to the sinus of the primitive heart.

A, dorsal view of auricular part of the human heart; B, corresponding view of wallaby's heart; C, corresponding view of the heart of a child in which the lungs were fused and the vestibule of the left auricle consequently unexpanded; D, corresponding view of the heart of a malformed fœtus in which the inferior vena cava was absent; E, corresponding view of the heart of the frog (Gaupp); F, corresponding view of the heart of the frog, the interior of the sinus venosus being exposed to show that the pulmonary veins open within the sino-auricular junction. In this figure, *p.o.*, orifice of pulmonary veins; *v.o.*, orifice of sinus venosus; *s*, attachment of interauricular septum; *s.a.j.*, sino-auricular junction. *v.*, vestibule; *r.a.*, right auricle; *l.a.*, left auricle; *s.v.c.*, superior vena cava; *c.s.*, coronary sinus; *i.v.c.*, inferior vena cava.

(2) *The Canalo-auricular*, marked by a thickening of the musculature round the ostium of the auricle, situated on the dorso-lateral wall of the auricular canal (2–2 in fig. 1).

(3) *The Canalo-ventricular*, marked in the mammalian heart by the auriculo-ventricular valves, the free margins of which separate the cavity of the auricular canal from that of the ventricle (4–4 in fig. 1).

(4) *The Bulbo-ventricular*, situated at the junction of the ventricle and bulbus (5 in fig. 1).

The Primary Divisions and Junctional Lines in the Mammalian Heart.—Our knowledge of the heart has been derived in great part from experiments made on the simpler hearts of the eel, frog, and turtle; in order to transfer accurately that knowledge to the mammalian, and more especially to the human heart, it is necessary to identify in them the primary divisions which are seen so clearly in the simpler hearts. We propose, therefore, in the first place, to identify the five primary divisions above mentioned in the human heart.

The Sinus Venosus of the Human Heart.—In fig. 2 is shown a series of illustrations of views of the sinus venosus in various hearts; the view represents the venous or auricular end of the heart, looked at from the dorsal side. The sinus (see E) is formed by the union of three great vessels—the right duct of Cuvier (*rt. sup. v.c.*), the left duct of Cuvier (*lft. sup. v.c.*), and the inferior vena cava (the hepatic vein of fishes). In the human and in the mammalian heart, the musculature of the auricular canal has grown over and submerged the greater part of the sinus (*o*, fig. 3); two parts only are left exposed on the surface of the heart—(1) the musculature of the superior vena cava, (2) the musculature of the coronary sinus (the representative of the left superior vena cava (see figs. A, B, C). But if a section be made across the line at which the sinus becomes submerged (the stria terminalis of His), a second or deep stratum of musculature is seen (beneath *o*, fig. 3); this probably belongs to the sinus venosus, since it extends beneath the endocardium of the auricle, from the position of one venous valve to that of the other. Besides these three definite remnants of the sinus musculature, there is also the musculature—or part of it—in the Thebesian and Eustachian valves, these being remnants of the right venous valve. There is often also to be found a thin muscular layer along the lower border of the fossa ovalis; it occupies the position of the left venous valve, and is probably derived from it. Thus, the chief remnants of the sinus venosus have to be sought for in the right auricle of the human heart. Its musculature is represented by:—

(1) The termination of the superior vena cava.
(2) The coronary sinus.
(3) The submerged stratum.
(4) The remnants of the venous valves.

It may be, however, that there are also remnants of the sinus in the left auricle of the human heart. In fig. 2, F, it is seen that in the heart of the frog the musculature of the sinus at the sino-auricular junction (*s.a.j.*) includes within it the orifice of the pulmonary veins. This is also seen in the heart of the malformed fœtus, fig. 2, D. It is possible, therefore, that, as the part of the auricular canal (*v.*) which is to become the vestibule of the left auricle expands, a part of this sinus musculature is also involved in the process, and may persist in the left auricle of the human heart around the orifices of the pulmonary veins.

In a part or in all of this sinus musculature the heart rhythm is believed to be initiated.

The Auricular Canal of the Human Heart.—In the simplest form of heart the auricular canal, which joins the sinus venosus to the ventricle, is differentiated into three parts (see fig. 1)—(i.) a basal part (opposite the auricle), (ii.) an annular part (3–3), (iii.) an invaginated or intraventricular part (4–4) The invaginated part forms an isolated layer beneath the auriculo-ventricular valves, its musculature becoming continuous with that of the ventricles near the apices of the valves (fig. 1). Only a small part of this musculature remains in the human heart; it forms the a.-v. bundle. This we shall treat of more fully later on. The annular part of the canal—the "auricular ring," as we shall term it in this article—has in the human heart become submerged in the auriculo-ventricular groove just above the

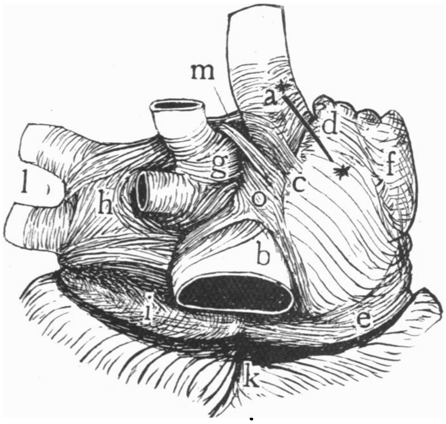

Fig. 3.—The auricular part of the human heart from behind, showing the musculature of the termination of the great veins.

***a*, superior vena cava surrounded by musculature derived from the sinus; *b*, inferior vena cava; *c*, to the right of the sulcus terminalis, above *c*, sinus fibres cross the sulcus to join auricle proper; *d*, at sino-auricular junction, where peculiar musculature is found most abundantly; *e*, annular fibres of auricle; *f*, appendix; *g*, fibres passing from interauricular septum to vestibule of left auricle between the two left pulmonary veins; *h*, vestibule; *i*, coronary sinus, showing continuity of fibres with right and left auricles; *k*, base of ventricles at interventricular sulcus; *l*, left pulmonary veins; *m*, constant band passing from sinus musculature to vestibule of left auricle; *o*, muscle of auricular canal submerging sinus; ** represent line of section of fig. 6, A.**

base of the auriculo-ventricular valves (*e*, fig. 3). Only one essential change has taken place. This can best be clearly explained by the help of a figure.

In the reptilian as in the amphibian heart (fig. 4, B) the annular part forms a simple ring; the interauricular septum lies within it, separating the right from the left a.-v. orifice. But in the mammalian heart the simple annular form has been lost; owing to the extension of the bases of the ventricles backwards under the basal wall of the auricular canal, the annular part has been folded as shown in fig. 4, A, so that the mesial folded part has now come to rest upon the upper or auricular margin of the interventricular septum. From this supraventricular fold of the annular ring begins the a.-v. bundle (stippled in fig. 4, A).

The basal part of the auricular canal is best defined by explaining its origin. The auricle or auricles are outgrowths from the dorsal wall of the auricular canal (see fig. 1); the ventral wall remains unspecialised as the basal part. The basal part, it will be seen, is continuous with the sinus venosus, with the ostium of the auricle, and with the auricular ring. From a physiological point of view the basal part of the auricular canal is most important, since both Gaskell and MacWilliam found that it was a path of conduction from the sinus to the ventricle, so that a sino-ventricular rhythm could occur. It is therefore interesting to see whether the possi-

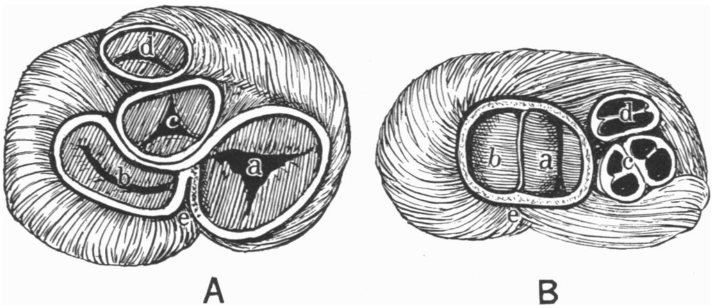

FIG. 4.—To illustrate the infolding and modification of the auricular ring in the mammalian heart.

A, base of the ventricles of human heart; B, base of the ventricles of heart of turtle. *a*, right auriculo-ventricular orifice; *b*, left auriculo-ventricular orifice; *c*, orifice of aorta; *d*, orifice of pulmonary artery; *e*, posterior part of the auricular ring, which becomes infolded in the mammalian heart. The stippled part near *e* represents the only part which remains undifferentiated in the mammalian heart.

bility of this rhythm remains in the mammalian heart. In the human, as in the mammalian heart, the basal wall has become profoundly modified by two great cardiac transformations which have occurred with the evolution of the pulmonary system. These changes are: (1) the formation of an interauricular septum, (2) the formation of a vestibule to the left auricle (figs. 2 and 3). The basal wall has supplied a large part, if not the whole, of these two structures. As the fibres of the lowest part of the interauricular septum come into intimate relation with the annular ring, it will be seen that it is therefore possible for a sino-ventricular rhythm to occur in the human heart. Indeed, a layer of longitudinal muscle fibres passes directly from the superior vena cava into the auricular septum, and thus reaches the musculature from which the a.-v. bundle commences. The musculature of the three parts of the auricular canal is represented in the human heart thus:—

(1) The basal part by the interauricular septum and by the vestibule of the left auricle.

(2) The annular part by the circular fibres surrounding the ostia above the bases of the auriculo-ventricular valves. The annular fibres also descend for some distance on the septal cusp of the tricuspid valve.

(3) The invaginated part by the a.-v. bundle.

The Auricles of the Human Heart.—In the fish's heart, the common auricle forms a well-demarcated outgrowth on the dorsal wall of the auricular canal. The ostium, by which it opens on the canal, is surrounded and indicated by a thick circular ring of musculature (fig. 1, 2–2). In the mammalian heart, the development of the interauricular septum and of the vestibule of the left auricle from the basal wall has led to a division of the auricle and to a wide separation of its two parts (see fig. 3). However, in the mammalian, and especially in the human heart, a prominent ridge of musculature, commencing in the right auricle immediately in front of the termination of the superior vena cava and seen on the roof of the left auricle, still unites the two auricles, and represents the original continuity of the two chambers (see fig. 7, A).

Thus in the right auricle of the human heart there is musculature derived from three sources—(1) from the auricle proper, (2) from the auricular canal, (3) from the sinus venosus. In the left auricle the musculature arises from (1) auricle proper and (2) auricular canal. All these parts are in the freest muscular continuity.

The Ventricle of the Human Heart.—It is unnecessary in this place to discuss the correspondence of the common ventricle of the lower forms with the divided ventricular chamber of the higher forms. They are developed as outgrowths from the ventricular segment of the primitive cardiac tube; the part which remains undisturbed between the outgrowths forms the interventricular septum. The upper margin of the septum represents the least disturbed part of the lumen of the primitive tube; on it lies the a.-v. bundle.

The Bulbus Cordis of the Human Heart.—This fifth division of the heart is well marked in the primitive forms (fig. 1, *e*). It is generally supposed to be absent in the mammalian heart, but recently Greil (3) and one of the authors (4) has shown that this is not so; the infundibulum of the right ventricle represents practically the whole of this cavity. The musculature of the bulbus has become replaced entirely or for the greater part by that of the ventricle.

The Musculature of the Sinus Venosus and of the Sino-auricular Junction.—Having thus sketched out, perhaps too briefly, the primary divisions of the heart, we now propose to describe the musculature of the sinus venosus and its connections with the other parts of the heart, more particularly in relationship to two points in physiology. (1) The rhythm of the heart begins in the sinus: does its musculature or any part of its musculature show any peculiar differentiation in connection with this function? (2) What are the muscular connections of the sinus; are they restricted so that a sino-canalar or sino-auricular "block" may occur, as is supposed by Wenckebach, or are they so wide and diffuse that such a block is inconceivable from an anatomical point of view? These two matters we shall discuss in relationship to the human heart, using our

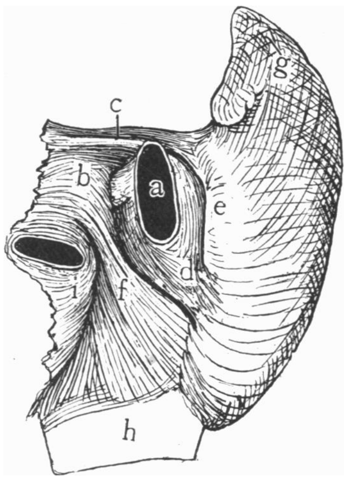

Fig. 5.—Right auricle of human heart viewed from above, to show connections of musculature at the termination of the superior vena cava.

a, superior vena cava cut across; *b*, vestibule of left auricle; fibres are seen to enter the interauricular septum from the superior vena cava; *c*, sinus musculature of superior vena cava passing to left auricle (*m* in fig. 3); *d*, sinus musculature of superior vena cava crossing sulcus terminalis to right auricle; *e*, sino-auricular junction; *f*, musculature of interauricular septum submerging sinus; *g*, appendix; *h*, inferior vena cava; *i*, septal fibres passing on to vestibule of left auricle below orifice of pulmonary vein.

comparative material only in so far as it throws light on the questions we discuss.

Taking the latter question first, we may say at once that the musculature of the sinus is freely continuous with that of the auricular canal and of the auricle. An impulse arising in the sinus musculature around the termination of the superior vena cava (fig. 3, *a*) may spread directly (1) into the musculature of the interauricular septum, and thus to the network in which the a.-v. bundle begins (fig. 5, *b*); (2) to the vestibule of the left auricle (*m*, fig. 3), and to the auricle proper along the inter-auricular bridge (fig. 5, *c*); (3) to the auricular canal of the right auricle; (4) to the right auricle proper (fig. 5, *d*). If the impulse commences in the coronary sinus, then it may spread directly (1) to the vestibule of the left auricle; (2) to the annular fibres of the left auricle; (3) to the annular fibres of the right auricle (fig. 3, *i*). Indeed, the higher one ascends in the vertebrate scale, the less becomes the amount of the sinus musculature, but the greater the closeness of its connection with the canalar and with the auricular musculature. It therefore appears to us that the sino-auricular "block" cannot be due to an anatomical lesion of a narrow bridge of fibres, but must arise from the depression, probably of vagal origin, of the muscular tissue in this region.

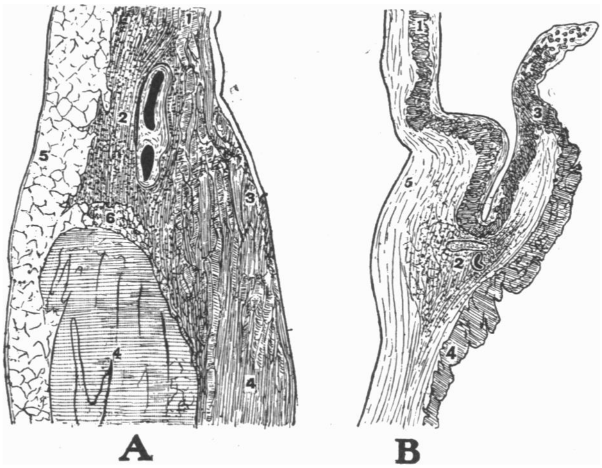

FIG. 6.—A, sino-auricular junction in human heart (position indicated in fig. 3); B, sino-auricular junction in turtle's heart. The figures represent corresponding parts in the two hearts.

1, musculature of superior vena cava or sinus in A; of sinus venosus in B; 2, artery and surrounding musculature at sino-auricular junction; 3, position of venous valve in A. In B, 3 indicates junction of musculature of sinus and auricle in the venous valve; 4, auricular muscle, differs from sinus musculature in both A and B in having a very slight endocardial covering; 5, sub-epicardial tissue; 6, connective tissue between sinus and auricle.

In fig. 6 we give two sections of the sino-auricular junction:[1] A is that of the human heart made across the sulcus terminalis in the position shown in fig. 3, B that of the heart of the turtle. The venous valve (see fig. 6, B) at the sino-auricular junction is seen to be really a fold of the cardiac tube; the musculature of one side of the valve is derived from the

[1] We use the term "sino-auricular" in preference to "sino-canalar" because, although a true sino-canalar junction exists on the dorsal side in the most primitive hearts (see fig. 1), yet in all but these the part of the canal between the sinus and the auricle disappears, and the dorsal junction becomes really a sino-auricular junction. Moreover, as the term "auricle" is usually applied in the mammalian heart to the parts representing both auricular, canal and auricle proper, the term "sino-auricular" is the more appropriate.

sinus—that of the other is continuous with the auricular musculature At the free margin of the valve the sino-auricular muscle is continuous (fig. 6, B, 3). A certain amount of fibrous tissue belonging to the epicardium is enclosed within the folds of the valve; in this an artery is frequently present. By the musculature of the valves an impulse may be freely distributed in the musculature of the auricular canal and of the auricle proper, for at the upper and lower angles at which the valves unite their musculature spreads out and joins freely with that of the auricular division of the heart (fig. 6, B, 4). In the mammalian heart a distinct remnant of the sino-auricular junction, so well shown in more primitive hearts, can be

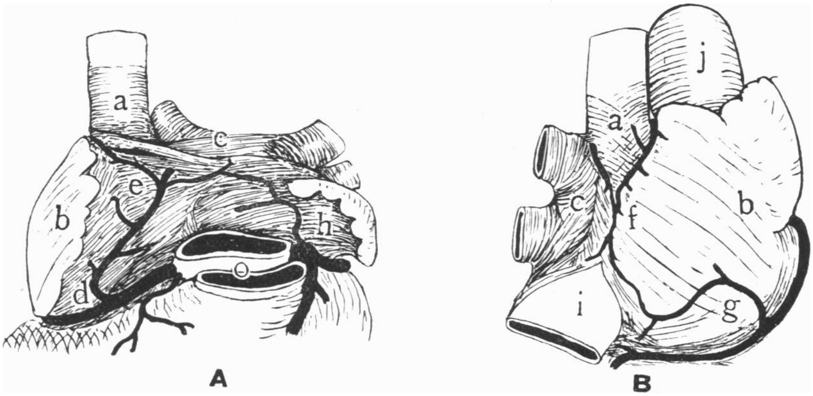

Fig. 7.—Showing blood-supply of the musculature of the sino-auricular junction.

A, aorta and pulmonary arteries removed, exposing auricles from the front; B, right auricle from the side. *a*, superior vena cava; *b*, appendix; *c*, vestibule of left auricle; *d*, artery arising from right coronary and passing to sino-auricular junction; at *e* the artery divides, one branch passing in the junction in front and the other in septum behind superior vena cava; *f*, union of two branches above mentioned in sulcus terminalis; *g*, anastomosing branch from right coronary artery; *h*, anastomosing branch from left coronary artery; *i*, inferior vena cava; *j*, aorta; *o*, aorta and pulmonary artery.

recognised (fig. 6, A). In the human heart, as in most mammalian hearts, an artery or arterial circle lies in the junction (fig. 6, A, 2); the artery is surrounded by fibrous tissue in which are numerous peculiar muscle fibres, some nerve cells and nerve fibres. The nerve cells and fibres we find from dissection to connect with the vagal and sympathetic nerve trunks which form so rich a plexus and exert so powerful an effect at this junction. The musculature of the superior vena cava becomes continuous with that of the auricle and of the auricular canal both on the outer and inner side of the artery.

Our search for a well-differentiated system of fibres within the sinus, which might serve as a basis for the inception of the cardiac rhythm, has led us to attach importance to this peculiar musculature surrounding the artery at the sino-auricular junction (fig. 6, A, 2). In the human heart the fibres are striated, fusiform, with well-marked elongated nuclei, plexiform in arrangement, and embedded in densely packed connective tissue—in fact, of closely similar structure to the Knoten. The amount of this musculature varies, depending upon how much of the sinus has remained of the primitive type; but in the neighbourhood of the tænia terminalis there is always some of this primitive tissue found. Macroscopically, the fibres resemble those of the a.-v. bundle in being paler than the surrounding musculature, *i.e.* in being of the white variety. They can be dissected out on the superior vena cava in the region corresponding to the right venous valve (*a*, fig. 3), and at the coronary sinus in the interval between it and the inferior vena cava and left auricle (*b*, *i*, fig. 3). Another remarkable point in connection with these fibres is the special arterial supply with which they are provided (fig. 7, A and B). These arterial branches, as noticed by Wenckebach, embrace the sino-auricular junction. It will be seen that they come from both right and left coronary arteries and form what may be termed the "sino-auricular arterial circle." We might mention also that, in some of the pathological hearts cut by us, sections of this region appeared to show a definite increase in the amount of fibrous tissue present—a fact of considerable importance, since we have found that the fibrous tissue of the Knoten and a.-v. bundle is sometimes increased in pathological hearts.

The nature of this remnant is perhaps best exemplified in the heart of the mole (fig. 8). Here it is seen that at the sino-auricular junction (A, E) there is a mass of remarkable tissue. It appears to the eye as a very intimate network of palely stained undifferentiated fibres with a large number of well-stained nuclei. It is totally different from the surrounding musculature, and contains but little fibrous tissue. Although the mass by its connections is undoubtedly muscular, the nerves in the neighbourhood of the superior vena cava appear to come into very intimate connection with it, so much so that we feel justified in stating that a highly differentiated neuro-muscular junction occurs at this point. In this heart also the bundle (I, fig. 8) is of absolutely identical structure.

In a section of the heart of the wallaby in this region there is seen under the low power (2″) a mass of fibrous tissue apparently separating superior vena cava from auricle. On closer inspection, however, it is seen that very delicate, palely stained, primitive muscular tissue is enclosed within the fibrous mass.

A section of this junction in the porpoise's heart is interesting. The musculature of the superior vena cava has largely remained primitive in type. The wall of the superior cava consists of alternate layers of fibrous tissue and primitive palely staining fibres. Just at the junction, however, of the superior vena cava and auricle, a network of these fibres and fibrous tissue is formed. In it there is an artery, and two nerve trunks lie close by.

In the dolphin's heart, on the other hand, there is no difference between the greater part of the musculature of the superior vena cava and that of the auricle. But in the region of the tænia terminalis there occurs some loosely-woven fibrous tissue, in the meshes of which are contained an artery and wavy, delicate muscle fibres with well-marked nuclei.

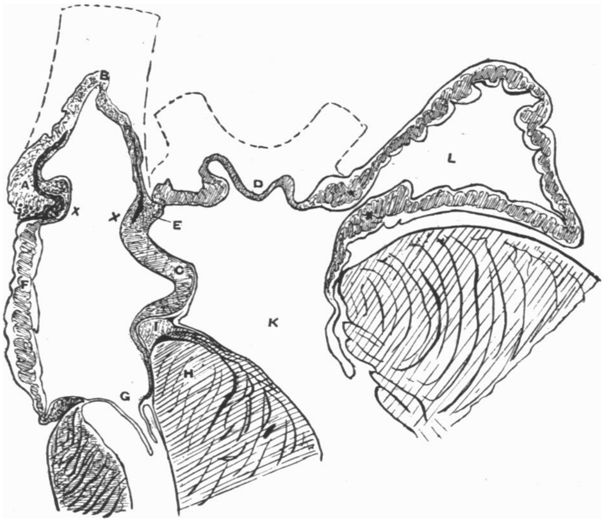

Fig. 8.—Coronal section of the mole's heart, showing position of musculature at sino-auricular junction.

xx, junction of superior vena cava and right auricle; A, peculiar musculature described in paper at sino-auricular junction; B, section of wall of superior vena cava; the position of the superior vena cava is outlined; C, interauricular septum; D, vestibule of left auricle; the pulmonary veins are outlined; E, similar musculature to A lying at junction of superior vena cava and vestibule; F, wall of right auricle; G, right auriculo-ventricular orifice; H, interventricular septum; I, a.-v. bundle similar in structure to A; K, left auriculo-ventricular orifice; L, left auricle **; canalo-auricular junction.

The ram's heart also shows a similar characteristic set of fibres in this region. The tissue in this case shows a marked amount of fibrous tissue loosely interwoven with palely-staining fibres closely resembling those of the sinus of the frog. The remnant also occurs in the hearts of the kitten, rat, and mouse.

From the above it will be seen that the presence of these primitive fibres is remarkably constant. Physiological experiments have clearly demonstrated that normally the heart's rhythm begins in the neighbourhood of the great veins, and that here nervous influence has a most potent effect (MacWilliam, Engelmann, Hering, and others). The fact, therefore, that there is a constant differentiation of certain fibres in this region, which, moreover, are in close connection with the nerves affecting the heart's rhythm, leads us to attach great importance to these fibres, and we feel justified in expressing the opinion that it is in them that the dominating rhythm of the heart normally begins.

The Canalo-auricular Junction.—At the ostium of the auricle in the lower hearts the musculature is directly continuous with that of the auricular canal (fig. 1, 2–2). In them there is a difference in the type of fibre constituting the two parts, those of the auricle being coarser, more striated, and more deeply stained. In the mammalian heart the junction between the parts representing the auricular canal and the auricle proper is also marked by a thickening of the musculature. The fusion of the different systems of muscle fibres, however, is for the most part so intimate that it is difficult to distinguish between them. We could find no trace of any especially differentiated fibres at this junction.

The Canalo-ventricular Junction.—This is the junction of the auricular canal with the ventricle. It has been described by MacWilliam in the heart of the eel. In this heart the auricular ring is connected to the ventricular system by the fibres of the invaginated part of the auricular canal (see 4–4, fig. 1). This part of the canal shows a differentiation even in the eel. Its fibres differ from those of the rest of the canal in being larger, less striated, staining more palely, and possessing a very large distinct nucleus.

In the frog there is a similar connection all round the auriculo-ventricular orifice below the base of the a.-v. valves, but particularly below the auricular septum. The fibres of the connection are not differentiated from those of the rest of the canal: they are shut off by fibrous tissue from the ventricular system in the upper part of their course, but later on they fuse with the fibres of the innermost part of the ventricular wall. The canalo-ventricular junction in the reptilian heart is similar to that of the fish and of the frog.

In the mammalian heart the auricular ring and the invaginated fibres become profoundly modified. Taking the human heart as a type, we find that the ring can still be traced round the right auriculo-ventricular orifice above the bases of the valves. The fibres are no longer isolated, but can be identified by their structure. No trace of them can be found in the canal of the left auricle. It will perhaps be well to recall the arrangement of the muscular connection between the auricular canal and the ventricle in the human heart. The system begins in the "Knoten," a small mass of interwoven fibres in the central fibrous body of the heart, having slender connections with (1) the musculature of the interauricular septum; (2) the circular fibres of the right auricular canal. From this arises the main bundle which passes along the upper border of the interventricular septum below the pars membranacea septi. Here it divides into a right and a left division, which pursue a subendocardial course in the right and left ventricles respectively, and finally fuse with the ventricular muscle. The fibres composing the main bundle, and more especially its arborisations, vary very much in type in the hearts of different species. In some hearts there is a marked difference from the ordinary ventricular musculature. Such is the case in the hearts of the sheep, ox, calf, cart-horse, pony. In these the main bundle consists of long, delicately striated fibres, with large nuclei. The end arborisations consist of fibres belonging to the Purkinje system. In other hearts the fibres of the bundle and its terminal branches are not so well differentiated from the ventricular fibres. This is the case in the whale, kangaroo, wallaby, dolphin, man, rat, kitten, mouse, shrew-mouse, and pig. In these hearts, however, and especially in the first four mentioned, there is still a differentiation of fibre rendering the bundle quite distinct from the ordinary ventricular musculature. The fibres of the bundle are larger, more delicate, less striated, and stain less deeply than those of the ventricle proper. In certain other hearts, namely, those of birds, the authors have been unable to find any differentiation of fibres in the bundle; the guides to it being its position and its definite demarcation by fibrous tissue. In the birds' hearts examined by us, the a.-v. bundle arises from the auricular ring and dives at once into the interventricular septum.

The a.-v. bundle is the sole muscular connection between the auricular canal and the ventricle; there is no direct connection between auricle proper and ventricle in the mammalian heart. It must be admitted, however, that in one case, namely, in the heart of a rat, the auricular and ventricular fibres appear to come into close apposition in the right lateral auriculo-ventricular region, and undoubtedly represent one of the connections described by Stanley Kent. In the heart of the sparrow also there is a similar close apposition of fibres in this region. This close apposition, however, cannot be looked upon as a connection; the a.-v. bundle is to be regarded as the sole connection between the auricular canal and the ventricle.

The Bulbo-ventricular Junction.—This junction is well marked in the primitive hearts (see 5, fig. 1). In all a circular groove containing epicardium separates the ventricular from the bulbar musculature, but not completely; the inner or subendocardial layer of ventricular musculature becomes continuous with the bulbar musculature. In the frog's heart this is also the form of connection, but the union is three or four times denser on the dorsal than on the ventral side of the b.-v. junction.

In the mammalian heart the bulbus has become fused with the right ventricle, forming the infundibulum of that cavity. Greil's research on the heart led him to the conclusion that, although the cavity of the bulbus remains, its musculature has been overgrown and replaced by that of the ventricle. The moderator band which passes from the septal wall of the right ventricle to the base of the anterior group of musculi papillares marks the separation of the bulbar part from the rest of the right ventricle. On this band of muscle the right division of the a.-v. bundle descends: that is, if our identification be correct, the right septal division descends in the position of the bulbo-ventricular junction. There can be no doubt, at least, that there is no bulbo-ventricular separation of fibres in the mammalian heart.

The Morphology of the A.-V. Bundle.—This is the third point which we had in mind during this research. As the result of our examination of the hearts in different branches of the vertebrate kingdom, we have come to the following conclusions in reference to the morphology of this bundle:—(1) The "Knoten" represents the only part of the annular ring of the auricular canal of the primitive heart which has remained undifferentiated in type. The rest of the ring has become differentiated and is imbedded in the other auricular musculature as explained above. (2) The main bundle and its two divisions represent the remnant of the invaginated portion of the auricular canal.

The chief evidence in favour of (1) may be summarised thus:—The different position occupied by the Knoten in relation to the central fibrous body in the hearts of different animals, *e.g.* of the sheep, horse, and man, points to the fact that in each a different portion of the auricular ring has remained undifferentiated as the Knoten. The musculature of the Knoten resembles in structure the other portion of the primitive canal which has remained undifferentiated, namely, the remnant at the sino-auricular junction, evidenced especially by the hearts of the mole, rat, and ram. Lastly, in the heart of a human embryo (32 mm. long) the auricular ring is clearly seen, and the part which is to persist as the Knoten is in close continuity with the ventricular musculature. The ring in this embryo is at the upper part of the interventricular septum, and its fibres are of exactly the same type as persist in the Knoten throughout life.

The evidence that the main bundle is the remnant of the invaginated portion of the auricular ring reveals itself as we proceed from the lower to the higher forms. In the eel this part of the auricular canal forms the a.-v. connection, which is all round the auriculo-ventricular orifice. In the amphibian and reptilian heart the connection is still around the whole orifice, but it is thickest at the base of the interauricular septum. In the bird's heart the connection is comparatively large, and is situated solely at the base of the interauricular septum. In the mammalian heart the connection is small, and occupies the upper border of the interventricular septum. It is beyond the purpose of this article to discuss the physiological reason for this restriction of the muscular connection between the auricle and the ventricle to a narrow bundle which measures on the average only $1{\cdot}5 \times {\cdot}8$ mm. in diameter; but its persistence in the position which it occupies becomes intelligible when it is called to mind that the upper border of the interventricular septum represents the least-disturbed part of the lumen of the embryonic cardiac tube.

Summary.

I. (*a*) The muscular connection in the lower hearts between sinus and auricular canal, and in the higher between the parts of the heart representing them, is intimate. In the latter, fibres pass directly from this junction to the vicinity of the a.-v. bundle.

(*b*) The canalo-auricular junction is marked by a thickening of the heart wall at this point. The muscular connection is diffuse. In the lower forms there is a difference between the fibres of the two parts, but in higher forms the fusion is so intimate that no difference in the type of fibre can be distinguished.

(*c*) The canalo-ventricular junction decreases in extent from the lower to the higher forms; in the latter it is represented solely by the a.-v. bundle.

(*d*) The bulbo-ventricular junction is well marked in the lower hearts. In higher forms the ventricular musculature has replaced that of the bulbus.

II. (*a*) There is a remarkable remnant of primitive fibres persisting at the sino-auricular junction in all the mammalian hearts examined. These fibres are in close connection with the vagus and sympathetic nerves, and have a special arterial supply; in them the dominating rhythm of the heart is believed to normally arise.

(*b*) No special differentiation of fibres was found at the canalo-auricular and bulbo-ventricular junctions.

III. (*a*) The Knoten is a part of the primitive auricular ring which has remained undifferentiated.

(*b*) The main bundle and its branches represent the invaginated portion of the primitive auricular canal.

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Note.—Since the above was written, Dr J. Mackenzie has kindly drawn our attention to a recently published paper of Hering's, "Ueber die Automatie des Saügethierherzens," in *Pflüger's Archiv*, Bd. 116, p. 143. It is interesting to note that Hering brings about complete stoppage of the supraventricular parts of the heart by a cut made at the sino-auricular junction in precisely the same position as our section (fig. 6, A).